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The Native Elm Bark Beetle

Hylurgopinus rufipes (Eichhoff)

In Connecticut

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The Native Elm Bark Beetle

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B. J. Kaston

Because of their importance in the dissemination of the fungus causing the Dutch elm disease, the habits of elm bark beetles have been studied by a number of investigators during the past few years. In Connecticut, investigations have been carried out particularly on the native elm bark beetle, *Hylurgopinus rufipes* Eichhoff. This beetle occurs throughout the entire State and is much more abundant than the European elm bark beetle, *Scolytus multistriatus* Marsham. Besides the then known distribution, as given in a previous paper (Kaston, 17), the species has since been recorded from Rhode Island, New Hampshire (Collins, *et al*, 8), Alabama, and Mississippi (Collins, 7). Its distribution is particularly significant when considered with the fact that a number of Dutch elm diseased trees have been found in outlying areas where the European beetle does not occur. These include Old Lyme, Conn.; Cleveland, Ohio; Baltimore, Md.; and Norfolk, Va.

Certain taxonomic considerations and a discussion of the morphology have already been published (Kaston, 17). The writer is indebted to Mr. W. O. Filley and Dr. R. B. Friend under whose supervision the investigations were conducted. He also wishes to acknowledge very considerable assistance from Mr. D. S. Riggs, whose aid both in the field and in the laboratory was practically indispensable. The photographs are the work of Mr. B. H. Walden and the drawings of Mrs. Elizabeth Kaston.

LIFE HISTORY AND HABITS

Emergence of Adults from Hibernation

If bark tunnels in which beetles hibernate are investigated during late April and early May, when the trees begin to leaf out, it will be found that they contain fresh boring dust. The beetles are active when disturbed and may even crawl out of the tunnels to walk about over the surface of the bark. Usually, however, the beetles dig further in the old tunnel before leaving to attack breeding material. By the latter part of May all hibernating tunnels are deserted, and beetles may be seen walking about over trap logs and attacking other attractive material.

Oviposition

Suitable material for oviposition may include any dying or dead (but not too dry) elm limb about two inches in diameter or larger. Occasionally a smaller limb, and quite often the trunk of a tree, may be attacked. In the latter case, if only one or two leaders are dying, the part of the trunk

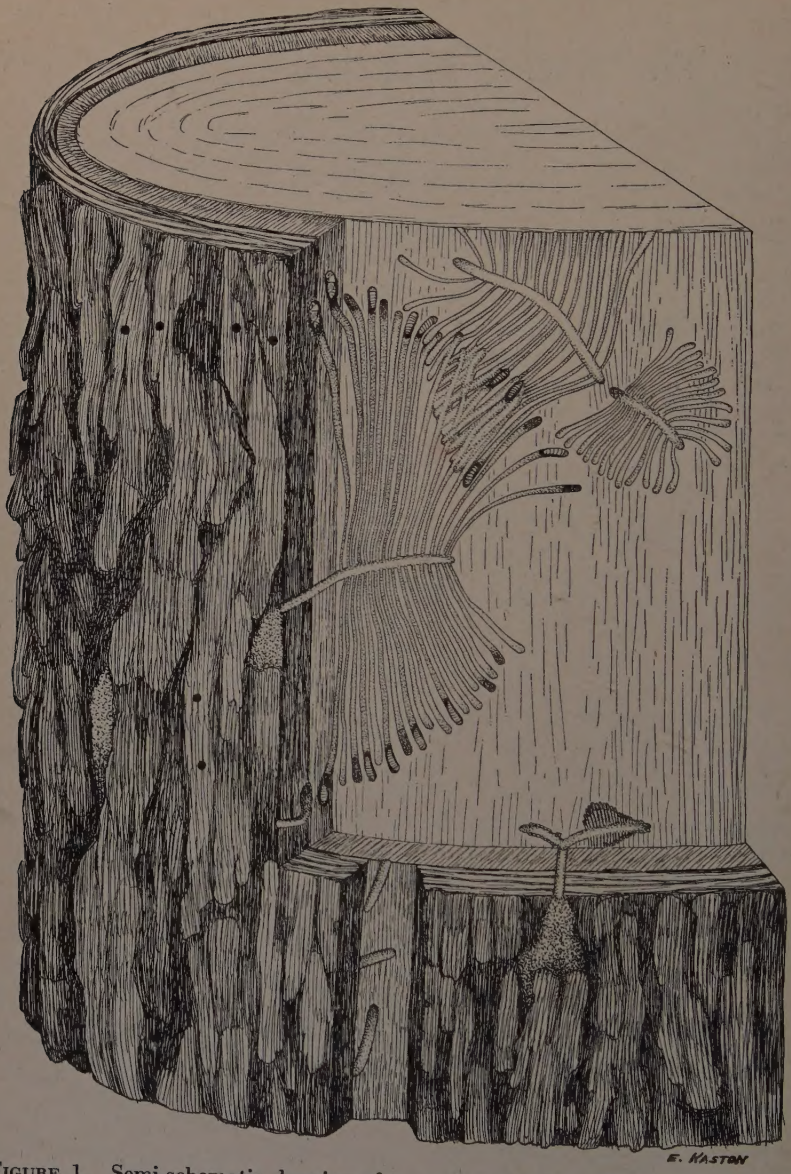

FIGURE 1. Semi-schematic drawing of a portion of a log. The bark is represented as having been cut through two entrance galleries, each with its accumulation of boring dust in bark crevices. Another entrance hole is evidenced by this frass accumulation on the bark near the left border. A short gallery with eggs and young larvae is shown near the lower right corner of the exposed wood surface. At the top of the exposed wood surface is a set of galleries, and to the left of this an almost fully developed family. Several occupied pupal cells are shown on the cut bark surface and an empty cell with an exit hole is inclined on the lower left. Several other exit holes can be seen. (Footnote continued at bottom of page 5.)

on which these grew may be attacked. Then there is usually a sharp demarcation between the portion still healthy, and the dying zone, with beetles restricted to the latter.

Trap logs were cut from healthy trees and set out in various localities. These were usually from 28 to 36 inches long, and from 3 to 8 inches in diameter. The localities selected were those in which elms grew in numbers, usually along streams and in swamps. Some were placed in deep shade and others where they could get full sunlight. Most of the logs were propped against the trunks of trees, but some were placed horizontally either on the ground or on a rack support.

Although logs were cut at intervals throughout the summer, very few beetles entered in August and September. Most of the attacks occurred in May and June. This agrees with the findings of Martin (24), who commented on the apparent paradox of the large numbers of young adults emerging from spring-laid eggs and their not entering suitable breeding places. This can be explained by the fact that the majority of newly emerging beetles first make bark tunnels in healthy trees. A discussion of this matter is reserved for a later section of this bulletin.

Several logs cut in the summer of 1935 and not attacked that year were left lying over until the succeeding year when they were attacked at the same time as the newly cut logs. Examination showed the bark to be quite moist and fresh looking.

The attractiveness of a log seems to be intimately related to its water content. Those left lying without any shade, where the heat of the sun could dry them rapidly, did not attract beetles. The undersides of the logs were more often attacked than the upper. In fact, the upper sides were seldom attacked unless in deep shade.

In one experiment a number of logs were weighed immediately after cutting and stored under diverse conditions for different lengths of time. After having lost weight in various amounts, they were weighed again when placed out to be attacked by beetles. Other factors being about equal, it was found that beetles did not enter logs which had lost more than 20 percent of their original weight. This is approximately half of the original water content, as determined by oven-drying samples from a freshly cut, healthy tree. These samples were cut from the lower trunk, middle trunk region, and the top of the tree, and included a complete disc of bark and wood. The average loss was 41 percent of the original weight. In this connection it may be mentioned that Martin (24) reported there is no correlation between the moisture content of the phloem and *Hylurgopinus* (and *Scolytus*) infestations. He did not explain just how the water content of this region was determined.

In addition to trap logs, several trees about 6 to 8 inches in diameter at breast height were girdled in 1935, in an attempt to make them receptive to beetles. Martin reported that his girdled trees were not infested, but he failed to state whether or not the trees had died. In our experience with 11 trees only one died the same season as girdled, and it was attacked by large numbers of beetles. Ten leafed out in 1936 and five of these died

In the center of the lower part of the bark a portion of the outer layers is removed to expose bark tunnels. (Note: Of course all these would not be seen at the same time in one log. Moreover, larval tunnels are not as conspicuous on the wood surface as indicated here.)

that year. The remaining five leafed out and died in 1937. After they died and before they dried out, these trees became attractive to beetles and large broods successfully developed in them.

Entrance gallery

The entrance tunnel of the adult beetle naturally varies in length with the thickness of the bark. The beetle selects a crevice in the bark or may get under an overhanging flap. Generally these tunnels are cut perpendicular to the outer surface and go directly into the wood surface (Figure 1). Often, however, they are inclined and approach the wood surface at an angle.

There seems to be no rule about which sex starts the gallery. Of 101 entrances examined during a period of about five weeks, 40 were being made by males and 61 by females. In addition, on five occasions "paired" beetles in entrance tunnels turned out to be two males, and on four occasions two females. There were also six instances of three beetles in one entrance hole. It would seem as if the eventual matching up of the sexes was a matter of mere chance. Some start entrance holes later to be joined by an individual of the opposite sex that has been wandering about over the log. After the egg gallery is started the normal condition is established, *i.e.*, the male nearer the entrance of the tunnel.

Egg gallery

Upon reaching the wood surface, the parent beetle constructs the egg gallery. Most commonly a biramous gallery is cut with the arms extending away from the entrance tunnel at various angles. While this egg gallery may be quite horizontal, it should be emphasized that more often it is inclined from the horizontal. Usually in a biramous gallery the inner end of the entrance tunnel forms the bottom of a "V" made by the two arms (Figure 1), though these may come off at any angle, independently of one another, and are seldom equal in length. In our studies on large numbers of galleries we found the biramous type most common, as indicated in Table 1. In some cases there is a shallow pit in one of the arms where the beetle has deepened the floor of the gallery. This is probably used as a turning place, as is also the entrance tunnel. The junction of the latter with the egg gallery probably also serves as a nuptial chamber. The egg gallery of this species scores the wood very slightly, and at times not at all, the parent then building entirely in the bark.

TABLE 1. TYPES OF EGG GALLERIES FOUND IN RANDOM SAMPLE OF 1745, ALL AT LEAST 10 MILLIMETERS IN LENGTH

Type	Number	Percent
Uniramous	221	12.5
Biramous	1428	82.0
Triramous	89	5.1
Quadriramous	7	0.4

The author has never been successful in seeing the mating of this species, despite thousands of galleries exposed in the course of this study. By analogy with other bark beetles one would expect that copulation takes place at the junction of the entrance tunnel and egg gallery. To determine when copulation had taken place, females were selected at different stages in the building of their egg galleries and dissected to see whether or not there were spermatozoa in the seminal receptacles. In this way it has been shown that mating may take place even before the building of the egg gallery. In general, however, the number of females with spermatozoa increases with the length of the gallery. In galleries of 10 millimeters or longer, *all* the females contained spermatozoa.

FIGURE 2. An example of a young egg gallery in which the eggs have been laid quite close together. (x 4).

The length of the egg galleries and the number of eggs per gallery varies. We have noticed that completed galleries in thick bark, as *e.g.*, on trunks, are longer than those in thinner bark. The longest seen was 77 millimeters, but the average appears to be 30 millimeters. Eggs may be laid closely packed on both sides of the gallery (Figure 2). Since the short diameter of the oval egg is about 0.4 millimeters, a maximum of five eggs per millimeter of gallery length (along both sides) is physically possible. This would allow very little space for packing frass, and ordinarily eggs are not packed so closely. The greatest density observed was 44 eggs in 9 millimeters of gallery, or 4.89 eggs per millimeter. This gallery was about 11.5 millimeters long at the time, but, as is usual, eggs were not laid within

2.5 millimeters of the entrance tunnel. Since frequently there are considerable spaces in which the female lays no eggs, the average density appears to be about two eggs per millimeter. Thus the average number per gallery, or per female, is about 60. This approximates the average found by actual count.

When beetles are abundant in the vicinity of suitable logs, many enter in a very small area. In especially attractive places on a log we have counted as many as 21.8 egg galleries per square decimeter over an area of 4.04 square decimeters. While this is exceptionally high, we have also counted 769 galleries on a log whose surface area was 47.32 square decimeters, or an average of about 16.3 per square decimeter. The average of 14 logs of assorted sizes which were used for complete counts, including emergence of the brood, was 4.4 per square decimeter. This would seem to be a moderately high average for attractive logs. From random sampling of trees in the field, the average would appear to be nearer 2.5 per square decimeter.

Rate of oviposition and period of incubation

Allowing three or four days for making the entrance tunnel, and another three or four for the first part of the egg gallery, the first egg is laid about a week after the entrance tunnel is begun. The female continues to lay as she extends the tunnel in length. As many as six eggs may be laid in one day, but the average is probably three or four during late June and early July. Because of the practical difficulty involved, we were unable to make actual observations on this process under normal conditions; hence we resorted to the following method. Many pieces of bark containing galleries with actively laying females were removed from the wood and placed in the constant temperature room. We noted the number from each family that hatched on any one day and assumed that these had probably been laid the same day. This, of course, is not strictly accurate, as it does not take into account the temperature at the time of laying. Moreover, it tends to give a low figure, for some eggs did not hatch. Hatching occurs in five or six days at a temperature of 25° C.

To determine whether or not females lay two sets of eggs the same season, logs containing adults with galleries having young larvae were caged with freshly cut logs. At intervals the logs were sampled to note the progress of the brood. At the time when the first pupae were beginning to transform to the adult stage, the fresher logs were removed and the bark peeled and examined for galleries. None were found in them. Moreover, most of the galleries in the old logs still had their parent beetles, and some of the latter were dead and moldy. These observations indicate that a female lays a single set of eggs a season, and that the parent beetles die that season. The discovery of egg galleries from which the parent beetles are missing cannot be construed as evidence that the beetles have gone elsewhere to lay. Rather, the possibility is strong that the parents have been killed and eaten by predators, such as, for example, *Enoclerus nigripes* Say.

Larval Period

When the larva hatches, it proceeds to feed in a line approximately at right angles to that of the egg gallery. Ordinarily this means parallel with the grain, but later it may deviate from that direction (Figure 1).

Digestion of cellulose

An attempt was made to ascertain whether or not the larvae could digest the cellulose present in the bark (and wood). Two techniques were employed. In one the gut was dissected out from each actively feeding larva, placed in a depression slide and teased apart in a drop of water. A minute drop of toluene for preservative and a single fibre of ash-free filter paper as substrate were placed in the mixture. The whole was then covered and sealed to prevent drying out. The slides were incubated at about 35° C. and examined each day. Of 20 such preparations observed over four days none showed any digestion of the cellulose fiber.

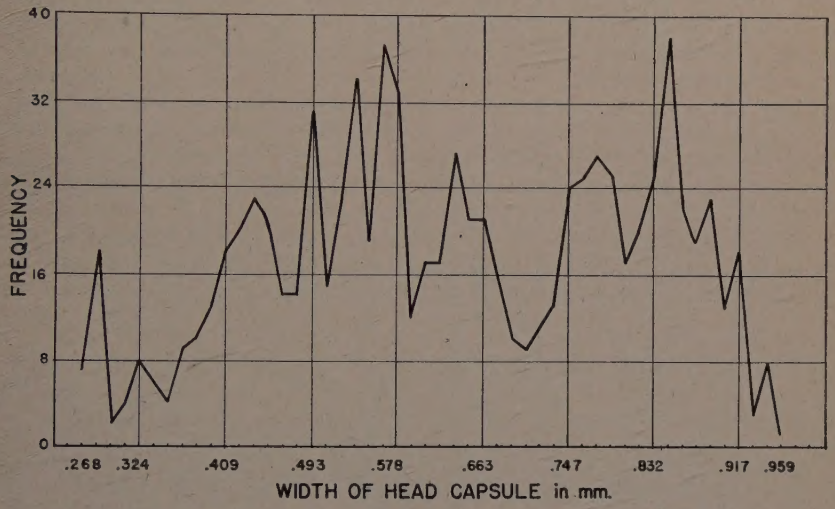

FIGURE 3. Frequency distribution of the head measurements of 853 larvae. These are mixed lots taken at random from various localities in the field. Each division on the abscissa equals .014 mm. (From Kaston and Riggs.)

In the second method the larvae were all ground up together in 10 parts by volume of 80 percent glycerine. The mixture was filtered at room temperature and only that filtrate used which came through in the first 24 hours. The mixture was then diluted to about 5 percent glycerine solution by adding an acetate buffer of pH 5. The resulting mixture was poured over pieces of ash-free filter paper and incubated at 35° in closed petri dishes. There was no digestion of the cellulose by this method either. It would seem, therefore, that the beetles had to derive their nutriment from the other constituents of the bark, the cellulose apparently passing through the digestive system unchanged.

Larval activities

In attempting to ascertain the number of larval instars, we first resorted to measuring the head widths of mixed lots of larvae taken at random from various localities in the field, as reported by Kaston and Riggs (21). This method has been successfully used by Blackman (4) on *Pityogenes*

hopkinsi Swaine, by Prebble (28) on *Ips pini* Say, *Pityokleines sparsus* Leconte and *Dendroctonus simplex* Lec., and by Bedard (3) on *D. pseudotsugae* Hopkins.

Larvae preserved in alcohol were measured to the nearest division of an ocular micrometer. They ranged from 19 to 68 units, or, as one division equals .014 millimeter, from .268 to .959 millimeters. The series of measurements of 863 larvae collected during the first season (1934) is shown in Figure 3. There is no distinct indication of a series of separate instars. The first peak is definitely known to represent the first instar, for many of these measurements were made upon larvae which had just hatched from the egg. From measurements made on specimens in the prepupal period it is known that the peak starting at about .817 millimeter and all higher than this definitely refer to the last instar. But the other peaks occur so irregularly that it is impossible to determine the number of instars between the first and last.

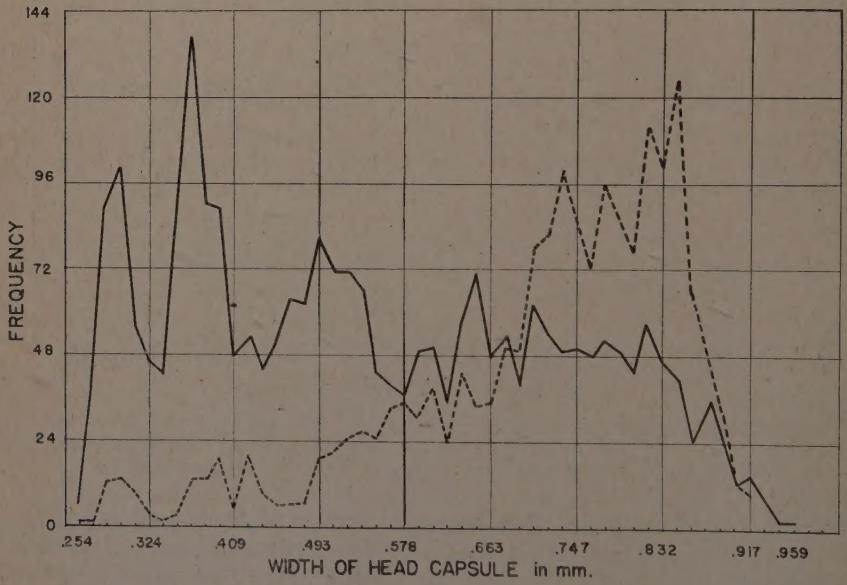

FIGURE 4. The broken line represents the frequency distribution of the head measurements of 1,816 larvae from a single tree. The solid line represents 2,598 larvae, the aggregate of those collected as single families. (From Kaston and Riggs.)

It was thought that perhaps a sample from a more restricted and uniform environment would give a clearer picture. Accordingly, during the second season (1935) 1,816 larvae from a single tree were measured. The broken line in Figure 4 represents this series. There is, unfortunately, a scarcity of younger larvae though the position of the first instar is sufficiently clear. As in the preceding figure, the position of the last instar is also clear, occurring in about the same place. Leaving out of consideration the lower instars, because of insufficient material, it is still impossible to demarcate the penultimate and antepenultimate instars in which most of the larvae fall.

During the third season (1936) it was decided to collect larvae by single families and plot each family separately. The ideal situation to encounter here is a family containing many larvae, with some in each instar. Figure 5 shows a histogram of a family of 75 larvae, one of the largest. Here can be seen distinct groups indicating the presence of five instars. Many other families showed a similar frequency distribution. On the other hand, there were a number of families which, though not containing individuals from all the instars, showed three or four groups of measurements arranged so as to indicate a total of six instars. In these the instars I and II occurred approximately as in the five-instar families. Moreover, the widths in the sixth or last instar were about the same as those of the last instar in the five-instar families. If all the families, totalling 2,598 larvae, are plotted together, we get a curve represented by the solid line in Figure 4. There is no doubt about instars I and II, but the remaining instars are difficult to delimit. When the two sets of larvae are mixed, as they might be in collections made at random, one might guess that there were possibly eight instars, a number which never occurred when individual families were plotted separately. This is a situation analogous to that which Gaines and Campbell (13) found for the black cutworm, some of which have six, and some seven instars. Of course, it does not follow that all the larvae in any one family will have the same number of instars, and in fact evidence was obtained from another source indicating that they vary. Our curves can only show what the predominant number appears to be for each family.

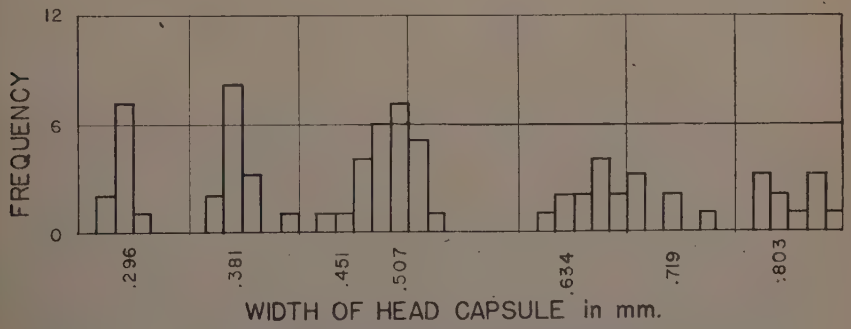

FIGURE 5. Frequency distribution of the head measurements of a single family of 75 larvae. (From Kaston and Riggs.)

By considering all the five-instar families, the mean head width for each instar has been calculated. From these can be calculated a growth ratio for each ecdysis, a mean ratio for all the ecdyses, and a set of theoretical mean head widths to test the possible application of Dyar's law. Prebble and Bedard had found that this law could be applied to the species they studied. Our findings are indicated in Table 2.

If one has only the first two instars from which to derive a ratio, the theoretical means would be those given in the fifth column. If the mean of all the ratios is used, the figures in the sixth column are obtained. As would be expected, the latter fall nearer the actual means than the former. Bedard had found for *D. pseudotsugae* that the mean head width for 200

TABLE 2. COMPARISON OF ACTUAL MEAN HEAD WIDTHS WITH THE THEORETICAL FIGURES OBTAINED BY USING A GROWTH RATIO

Instar	Variation mm.	Actual Mean mm.	Growth Ratio	Theoretical Mean	
	Five-instar Families			*If Ratio=1.322*	*If Ratio=1.303*
I	.254—.324	.286±.010		.286*	
			1.322		
II	.324—.437	.375±.013		.375*	.372
			1.343		
III	.423—.592	.506±.024		.500	.496
			1.303		
IV	.564—.761	.646±.029		.661	.632
			1.242		
V	.705—.931	.821±.031		.875	.824
	Six-instar Families			*If Ratio=1.263*	*If Ratio=1.239*
I	.268—.324	.287±.012		.287*	
			1.263		
II	.324—.423	.363±.015		.363*	.356
			1.229		
III	.409—.507	.445±.017		.459	.441
			1.274		
IV	.521—.649	.567±.023		.579	.544
			1.253		
V	.634—.832	.711±.026		.731	.625
			1.177		
VI	.747—.959	.837±.035		.922	.835

* Mean by actual measurement.

larvae in the first instar was .523 millimeter, and for 200 in the second, .615 millimeter. The ratio between these is 1.175, and if one attempts to determine the succeeding instars on the basis of this ratio one obtains seven, with the mean width of the last 1.37 millimeters. This falls between his observed actual mean of 1.38 and the theoretical 1.34. Yet he shows definitely that there are only five instars in this species, so that use of the ratio between the first two instars to determine the number succeeding leads to error.

Becker (2) believes that five instars is the usual number for *H. rufipes*. He considers that the irregularities in the peaks which appear when the head widths of the *later* instars are plotted may possibly be explained by assuming a variation in size of the two sexes. His measurements of the heads of adult beetles indicate a difference of about 10 percent. Our own figures based on 102 males and 115 females indicate the latter to be only about 6 percent wider. But even a 10 percent difference, if such existed in the larvae, would hardly account for the irregularities in the peaks.

To estimate the approximate duration of each larval stadium, Prebble had taken the interval between the date when the particular instar formed the majority of the population, and the date when the succeeding instar formed a similar proportion of the population. Bedard, using Taylor's method, counted the number of days from the first appearance of one instar to the first appearance of the next and the number of days between

the last dates of appearance of the same two instars, added these two numbers together and divided their sum by two. Our analyses of the series of head measurements according to dates of collection showed that practically all stages could be found in random samples at any time during the season. Hence it is evident that neither of these methods could be used successfully here.

In order to get more accurate information about larval activities we prepared a device which enabled us actually to watch the larvae from day to day. For the best results a piece of bark is selected which contains a large number of eggs in a gallery, at least several inches removed from other galleries. The outer bark is removed from a rectangular area of about three by five inches, after which the external surface of the inner

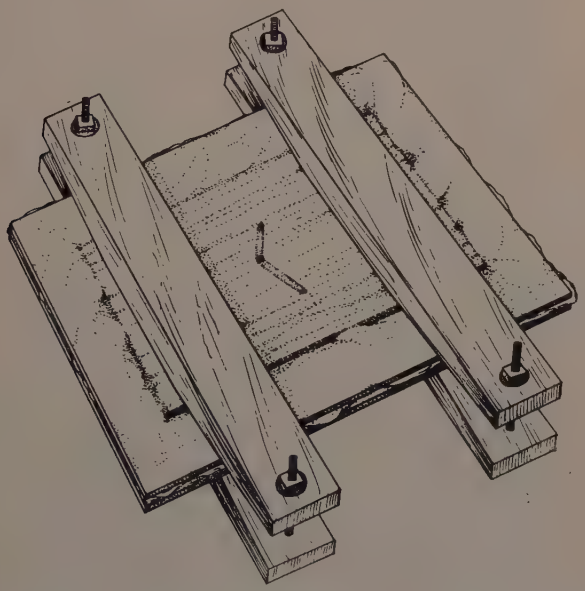

FIGURE 6. Device for rearing larvae so as to keep them under daily observation. Explanation in text. (From Kaston and Riggs.)

bark is smoothed off as much as possible. It is essential that this be done in order to have the piece of uniform thickness throughout. The piece is now removed from the tree or log and immediately placed between two plates of glass. The parent beetles, if present, should be removed first, and care must be taken that none of the eggs (or young larvae) are displaced. It requires considerable pressure to keep the plates close to the bark, and thus prevent warping with the subsequent falling of the active larvae out of their tunnels. The success of this rearing method depends in large measure upon keeping the inner surface of the bark in intimate contact with the glass. Elastic bands, as used by Bedard in a similar apparatus, were not satisfactory, so we resorted to the device illustrated in Figure 6. Four strips of wood, each about 7.5 inches long by 1.25 inches wide by .5

inch thick, were prepared to serve as two pairs of clamps. Bolts were placed about a half-inch from each end and the pieces of wood were beveled so that only the center 2 inches of each was in actual contact with the glass. In this way, on tightening the nuts, pressure was applied only directly over the bark. It was found that the larvae got along best when the bark was kept quite damp, so cotton was packed around the bark and moistened daily. When not under actual observation, the entire device was wrapped in black cloth or paper and kept at an approximately constant temperature of 24° C.

FIGURE 7. Live larvae and their frass trails as seen through the glass of the observation rearing device, (x 6). The larva second from the left has been underneath for some distance and the place where its frass trail again strikes the surface is plainly seen. (From Kaston and Riggs.)

With this apparatus it was possible to watch, for various lengths of time, the progress of 31 families, including 374 larvae. The dates of hatching were obtained for 218 eggs, the dates of ecdysis accurately known in 552 instances, and estimated in about another hundred. Of the 50 larvae that succeeded in pupating, the time of hatching was obtained for 28, so that the duration of their entire larval life was known. Moreover, the number of instars and duration of stadia are known from *direct observation.*

There is a very strong tendency for the larval tunnels to run with the grain (Figure 7). Even when the egg gallery is not transverse, but inclined,

the larval tunnels, which start off at right angles to this, almost immediately diverge from their original direction to become longitudinal. However, there are instances where the larval tunnels, especially those nearest the ends of the egg gallery, bend in a curve toward the latter. In the case of a female completing one arm of a V-shaped biramous gallery before laying any eggs in the other arm, the larvae hatching later almost always eventually encounter the frass trails of older members of the family. If, as Trägårdh (33) believes, the larva is able to detect the degree of decomposition or dryness of the surrounding bark and thus be guided in the proper direction, there is the apparently aberrant behavior of occasional larvae suddenly changing direction and crossing the frass trails of neighboring larvae, or even proceeding back toward the egg gallery in their own or another's frass trail! Yet a larva never failed to change its direction whenever it approached the cut edge of the piece of bark.

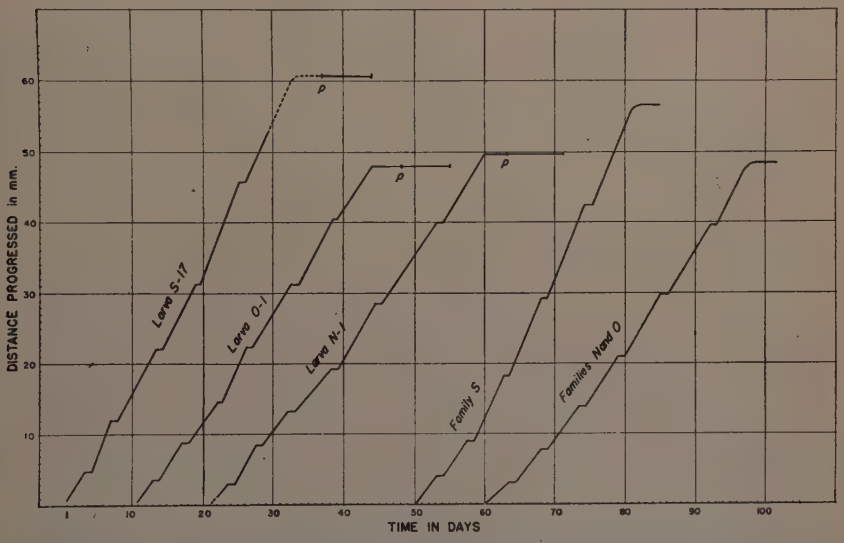

FIGURE 8. Progression curves of three different larvae, as well as of the mean determined for three families. The "p" indicates the place at which pupation occurred. (From Kaston and Riggs.)

By measuring the length of its tunnel each day, a curve can be plotted for each larva, such as is shown for three individuals in Figure 8. It was found that accompanying each ecdysis there is a period of almost a day during which the larva does not feed. This is represented by a short horizontal line along the curve. Also obtainable from these curves are the total duration of larval life, the duration of each stadium, and the number of stadia. For example, larva N-1 had seven stadia, the duration of which and the distance progressed during each being as follows:

Instar I,	4 days,	2.5 mm.	
II,	5 days,	5.3 mm.	
III,	4 days,	5 mm.	
IV,	6 days,	6.1 mm.	
Instar V,	7 days,	9.3 mm.	
VI,	7 days,	11.4 mm.	
VII,	11 days,	10 mm.	

It did not tunnel for about three and a half days before pupation, and remained eight days in the pupal stage. In like manner, larva S-17 went through six instars in 36 days, tunneling a distance of 60.8 millimeters. Between the twenty-ninth and thirty-third days it was not visible (indicated by the dotted line in the curve), having gone underneath the surface of the bark. It was later dug out on the day of pupation at a point 8 millimeters beyond the point at which it had disappeared.

The larvae of families N and O taken together present a curve showing a much slower rate of tunneling than those of family S. These curves also show what has been found true in general for the other families as well, namely that there is a positive correlation between the number of instars and the duration of the larval period. Larvae have completed their development in 6 to 12 instars, and in Table 3 is indicated the mean duration of the larval period.

TABLE 3. MEAN DURATION OF LARVAL PERIOD

Number of instars	Duration	Number of larvae
6	35	7
7	42	7
8	49	2
9	64	1
10	71	3
11	89	1
12	85	1

The instances of 9 to 12 instars all occurred in family A, which developed under abnormal conditions. It was one of the first families reared, and the bark was not kept tightly against the glass at all times. This resulted in drying of the bark alternating with flooding when an attempt was made to remedy the situation. This shows, however, that the larvae are potentially capable of molting more than the normal number of times. Some of the irregularities in our curves (Figures 3 and 4) may be due to retarded larvae which are going through a greater number of instars. In this connection it is of interest to note that Metcalfe (26) was unable to arrive at any satisfactory conclusion concerning the number of instars in the anobiid, *Sitodrepa panicea* L. The curve of head-capsule measurements plotted from random collections presented nine peaks which the author hesitated to accept as representing a like number of instars, "a number hitherto unprecedented in the Coleoptera." Instead, evidence was presented to indicate that four of the peaks belonged to one sex and five to the other.

There seems to be no correlation between the distance tunneled and the duration of larval life. However, the mean of the distance traveled increased in successive instars, as is to be expected.

Different larvae showed great variation in their rate of tunneling, as shown in Figure 9. Here the slope was obtained from curves similar to Figure 8 simply by connecting the point representing the time of hatching with the point where the larvae stopped tunneling in preparation for pupation. For larvae A-4 and A-10 these curves extend to the time of pupation. Larva N-2 went underneath the bark surface during the seventh stadium so that the dotted line was continued from this point to the day when the average for this family pupated. Larva Q-d was lost to view during the sixth stadium, the dotted line indicating the *probable* course to pupation, the average duration of larval life not being known for family Q. It can be readily seen that larva A-10 had traveled about 13 millimeters in the first 20 days, whereas larva N-2 had gone just about twice that far, and larva Q-d about three times.

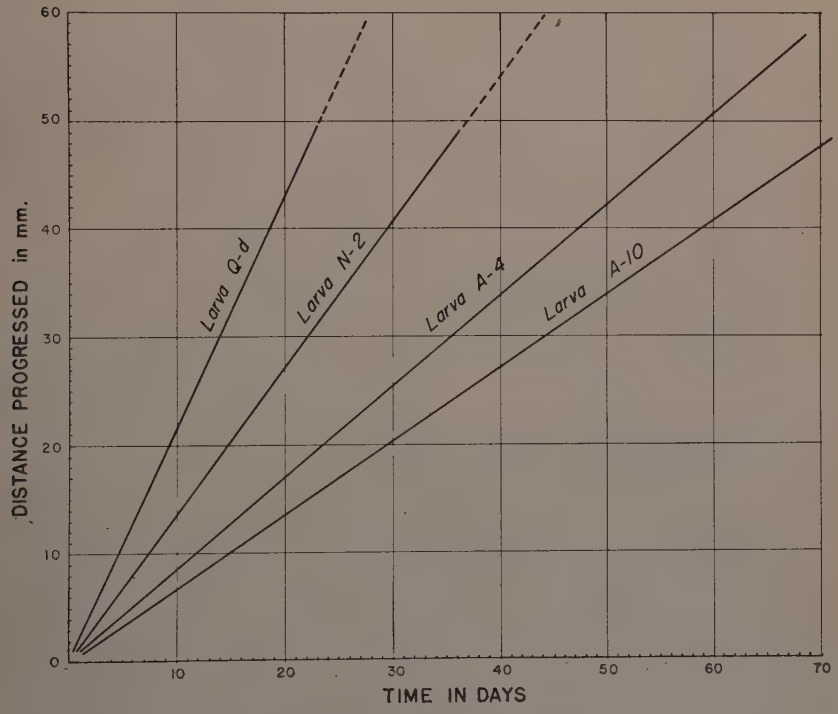

FIGURE 9. Rate of tunneling of various larvae. Explanation in text. (From Kaston and Riggs.)

After molting, and when the new head capsule has hardened, the larva turns around in its gallery and eats the exuviae. Blackman suggested that the larvae of *P. hopkinsi* have the same habit because he did not always find their exuviae in the frass trails. Prebble had likewise encountered similar difficulty with the three species previously referred to. However, we have found that only the relatively soft body cuticula is eaten, leaving the head capsule. This gets broken up so that only certain parts, especially

the mandibles, may be distinguished later. At intervals the larva turns around and packs the newly voided frass with its head, using its mandibles to tamp it down firmly. During this process the remains of the capsule often become buried or obscured. With material brought in from the field we have found it possible, by careful manipulation under a binocular, to expose fragments at intervals in the tunnels. The discovery by this method of five groups of capsule fragments in a few tunnels indicated to us that there could be at least six instars. Since the fragments are pushed about in the frass trails, it is not possible to deduce from their spacing how far the larva travels during each stadium.

Pupal Period

Before pupation the larva in the last instar spends about a day and a half during which it does not progress farther, but simply enlarges the end of its tunnel to form a pupal cell. This may be called the ante-prepupal period, and is followed by a prepupal period during which the larva is quiescent for almost two days. It shortens slightly, loses some of its curvature, becomes creamy white, and thickens around the thorax.

The pupal cells are almost always built in the inner bark alone. They are seldom in contact with the wood surface, more often touching the outer bark. Very rarely, especially when the log is quite dry, the pupal cell may be entirely in the outer bark. The oval cell is built with its long axis parallel to the grain of the bark (Figure 1).

In the constant temperature room (about 24.5° C. and 65 percent humidity) the average duration of the pupal period is 7.26 days. On the first day, the pupa is entirely white. On the second, there is a faint suggestion of pigment in the eyes. On the third, the eyes are faintly tan. On the fourth, they are brown to red; on the fifth, dark brown to black; on the sixth, the mandibles acquire a brownish-red color, and the wing tips become gray. On the seventh, the legs, head, and pronotum become orange. Emergence from the pupal skin takes place while most of the body is still white. After emergence the callow adult colors up rapidly before beginning to cut its way out of the pupal cell. The pupal stage under field conditions in July is estimated to be eight or nine days in length.

TABLE 4. DURATION OF PUPAL STAGE AT VARIOUS TEMPERATURES

Temperature degrees C.	Number of pupae	Number emerged	Percent emerged	Number of days pupation
10	94	3	3.2	57.7
13	..	7	....	23.3
15	67	18	27	20.5
20	78	18	23	10.94
24.5	..	46	....	7.26
25	36	21	58	6.81
30	55	36	65	5.42

Since the pupal stage is quiescent, it is a relatively easy matter to test the effects of different temperatures on the rate of development. The prepupae were removed to dishes and placed in incubators at various temperatures. The figures in Table 4 indicate the results obtained, and the results are shown graphically in Figure 10.

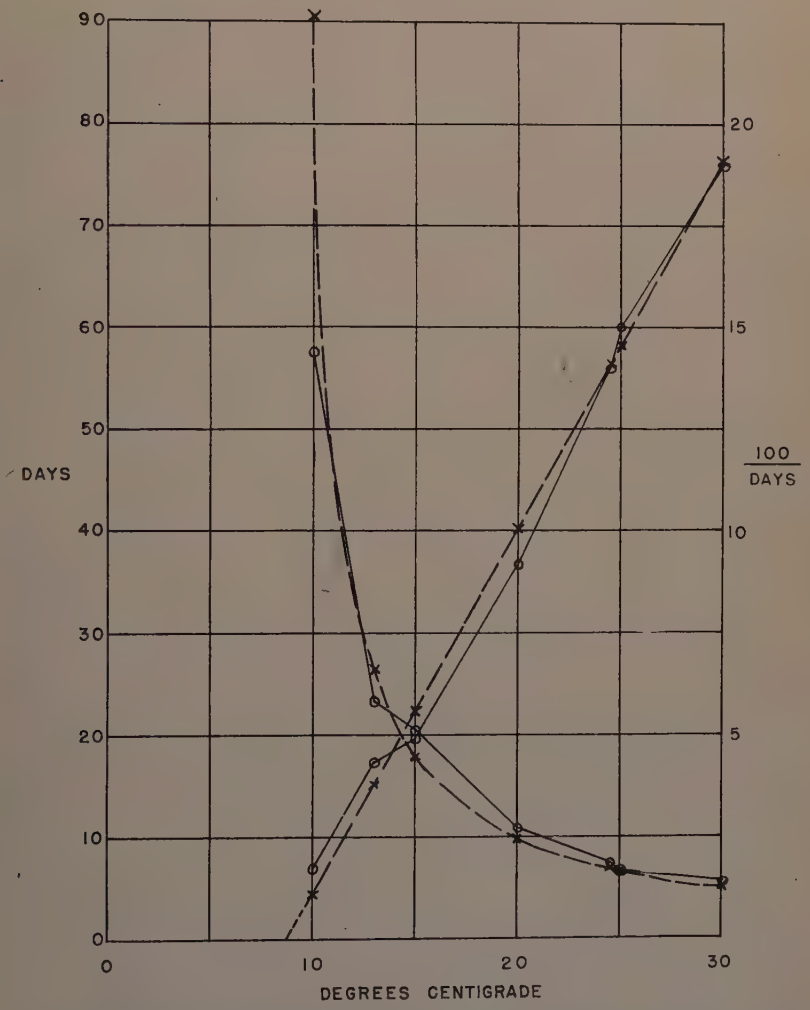

FIGURE 10. Effect of temperature on the development of pupae. The solid lines follow the actual data. The broken lines indicate the following theoretical curves: hyperbolic: K = Time × (Temp. -8.8); rectilinear: $\frac{100}{\text{Time}} = .9 \text{ Temp.} - 7.9$.

The time-temperature relations of insect development have been expressed frequently by the formula K = Time × (Temp. —Z), where K is a constant and Z is the "physiological zero". This is the formula for an equilateral hyperbola. Although it probably does not represent the true conditions at the upper and lower temperature limits at which development can occur, nevertheless it does represent the effect of temperature on insect development within certain limits. The data given in Table 4 fit rather well the formula K = Time × (Temp. —8.8), and the hyperbolic curve in Figure 10 represents this formula. The greatest divergence of the theoretical from the actual is at the 10° level. At this temperature relatively few pupae survived, and it is so close to the "physiological zero" that slight divergences are accentuated.

The reciprocal curve, where the temperature is plotted against the reciprocal of time, illustrates the effect of temperature on the rate of development. This curve is rectilinear and is also shown in Figure 10. The data correspond rather well to the formula $\frac{100}{\text{Time}} = .9 \text{ Temp.} - 7.9$ (the reciprocal of time is multiplied by 100 to avoid decimals). The curve has been projected to meet the X axis at the theoretical "physiological zero", 8.8° C.

It appears that pupal development will not take place at temperatures below about 8.8° C., but such development will certainly occur at temperatures exceeding 30° C. Between 10° C. and 30° C. the rate of development is directly correlated with temperature, and the relation of increase in developmental rate to increase in temperature may be expressed by a rectilinear equation. Pupae held at 5° C. for 60 days showed no signs of development, no pigment appearing even in the eyes. When removed to 24.5° C., 11 of the 64 specimens emerged normally in 7 days; the others died. The mean number of days taken for pupae held continuously at 24.5° C. was 7.26. This supports the contention that the so-called "physiological zero" for pupae is at about 8.8° C. (about 48° F.).

Emergence of Adults from Bark

After the callow adult has hardened somewhat, it gnaws its way to the outside. The exit tunnel is ordinarily cut at right angles to the surface and the beetle emerges through a "shot" hole of about 1.25 millimeters diameter (Figure 1). In some cases, where the outer bark is somewhat loosened from the inner, the beetles cut through to the outer surface of the inner bark and groove this surface between the two bark layers until they can emerge through a crack, or at the broken end of the log, etc. Selecting a random sample of several hundred, the sexes were found to be about equal in numbers.

By placing logs in cages and checking regularly, one can count the number of adults that emerge each day, and it is possible to determine the time of the peak emergence. In the accompanying graph, Figure 11, the emergence curve for log number 373 is shown. This log was enclosed with about 275 beetles and kept in a constant temperature room at about 24.5° C. during the entire period of development. Young beetles emerged over a period of 52 days of which the first occurred 57 days after the log was exposed to attack. The peak of emergence occurred at about

74-75 days, or 17-18 days after the first beetle emerged. The shape of the curve follows that of a normal curve, superimposed upon it in the graph, but there is a tendency for late emergences to be prolonged for a considerable period.

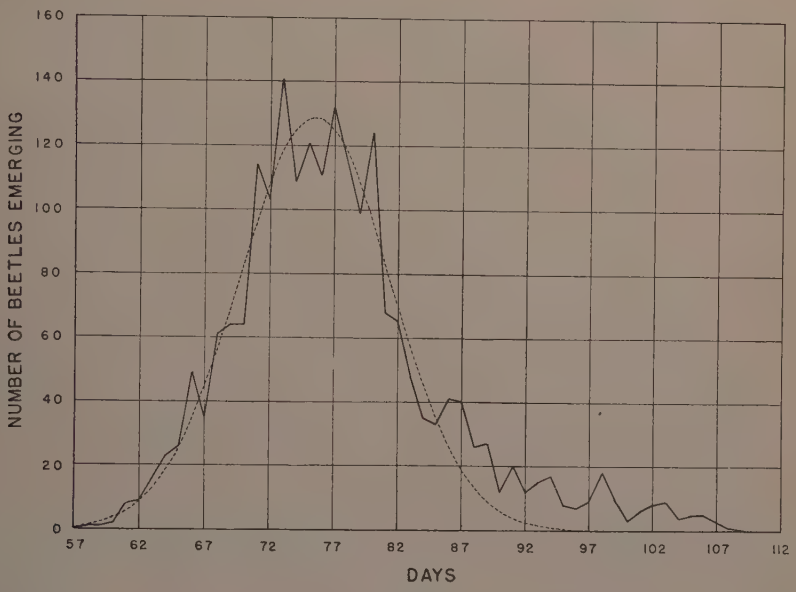

FIGURE 11. The solid line represents the curve of emergence of young adult beetles (which were kept at a uniform temperature for the entire period of their development) beginning at 57 days after the log was subjected to attack. The approximation of this to a "normal" curve is indicated by including the latter as the broken line.

Emergences from logs in nature are usually spread over a period of two months or more, and during the peak the number each day is roughly correlated with the temperature. Figure 12 indicates this correlation (for a portion of the emergent period) in the case of two logs caged in an outdoor insectary. The first beetle emerged August 2, though the peak of the emergence is about the third week in August. Somewhat similar results were obtained with other logs in previous seasons, a small emergence starting just after the middle of July and the peak occurring in either the second or third week in August. This, of course, refers to progeny from spring-laid eggs.

It is difficult to determine just how many beetles come from any one family. The egg galleries are usually placed so closely that the larval tunnels and exit holes of neighboring families intermingle. By the time the brood emerges the larval tunnels are not distinct and cannot be counted. It then becomes necessary to obtain an average by counting exit holes, removing the bark and counting the egg galleries. These figures are supplied in Table 5.

The logs selected were those which appeared to have "normal" galleries and which had not dried too much. Of 14 logs examined after the broods had emerged the highest average was 21.5 young beetles per family, and the lowest was 11.9. The mean of these averages is 15.6. Since, as already stated, the average number of eggs laid per female is about 60, this indicated that the hazards of life under field conditions from egg to young adult reduce the population 75 percent. A reduction of 85 percent was reported for *Dendroctonus brevicornis* Leconte by Keen and Furniss (23).

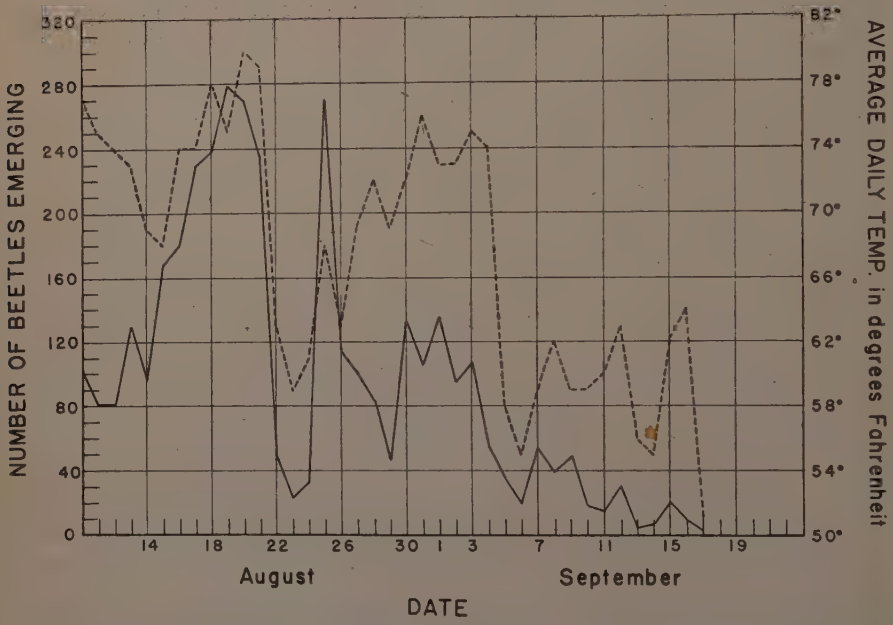

FIGURE 12. The solid line represents the number of young adult beetles emerging. The broken line indicates the average daily temperature.

Occasionally, when a piece of bark is removed, it is found to contain a family in which the larval tunnels are not confused with those of neighboring families. From one such, of which the egg gallery was 20 millimeters long, there emerged 27 young beetles; and in another, 11 millimeters long, there were 14 exit holes.

Flight and Wind Carriage

To obtain information on the flight powers of the beetle we set up trap logs in two elm-free areas. The first of these was a sand bar projecting out from the mainland proper at Old Lyme. Freshly cut logs were suspended from tripod arrangements so as not to touch the sand, and shade was provided for each log. The logs were placed at approximately 300-yard intervals extending south and west of the nearest elms. On three occasions a beetle was collected at a log three-fourths of a mile out.

The second of these elm-free areas was Charles Island, approximately three-quarters of a mile off the Milford coast. The nearest elms are about

one-fourth mile back from the coast. Two beetles were recovered from one log and one from another. Hence they must have flown about a mile, though it is possible, of course, that they were blown by the wind. Felt has shown in a series of papers (9, 10, 11) that even heavy-bodied insects like beetles can be distributed by the wind. His experiments with balloons also indicate that the prevailing winds in this region are northeast. There is thus the further possibility that the beetles taken from the logs in our elm-free areas may have come from farther away than the nearest elms, for the latter were north and east of the trap logs.

TABLE 5. ADULTS EMERGING PER FAMILY FROM LOGS

Location	Log number	Number of families	Number of exit holes	Average number young beetles per family
Riverton	2	148	1764	11.9
Riverton	7	90	1603	17.8
Riverton	4	25	456	18.3
Riverton	120	140	1882	13.5
West Hartford	271	166	3562	21.5
Orange	321	106	1685	15.9
Orange	320	130	1933	14.9
Franklin	378	117	2086	17.8
Franklin	379	124	1816	14.6
New Haven	351	42	515	12.2
New Haven	353	41	652	15.9
New Haven	373	92	1536	16.7
Cheshire	380	177	2387	13.5
Cheshire	383	125	1863	14.9

It is probable that emerging beetles will not attempt to fly long distances, but rather are attracted to the nearest satisfactory elm material. This is indicated by the fact that bark tunnels in healthy trees are more numerous the nearer the trees are to logs from which beetles have emerged.

Bark Tunnels in Living Elms

Within 24 hours of their emergence from the bark, the callow adults may enter logs to breed, as indicated by their behavior in the insectary, but we have found that large numbers of them will first fly to nearby healthy elms and feed there. Experiments during the 1935 season showed that when a number of beetles were enclosed in a cage containing only freshly cut twigs, they made feeding tunnels similar to those known to be made by

Scolytus multistriatus, but when freshly cut logs of three- to six-inches diameter were also provided, they tended to attack the latter rather than the twigs. Accumulations of frass in crevices of the outer bark may lead one to suspect that the beetles have burrowed in to build egg galleries. But if such a place is investigated thoroughly, it will be found that instead of an entrance hole leading to the wood surface, there is a shallow tunnel more or less parallel to the surface, just under the outer bark (Figure 13).

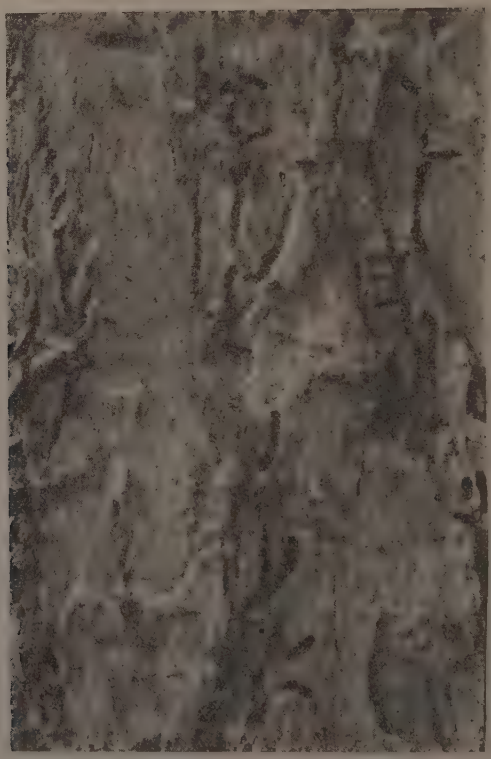

FIGURE 13. Surface view of a portion of trunk showing bark tunnels natural size. (From Kaston and Riggs.)

Those beetles which develop from overwintering larvae will be found making such bark tunnels in early to middle June. But those which emerge from eggs laid in the spring and early summer will be found in largest numbers in August and September. Many of these latter will not start brood galleries until the following year, but will hibernate in the bark tunnels on the healthy trees (Kaston and Riggs, 22).

In 1937 the first bark tunnels were observed in the field on July 22, which was shortly after the young beetles had started emerging. From July 30 to September 3 live elms were examined at intervals of three or four days. During this period notes were taken on a total of 291 bark

tunnels in the tops, trunks, and exposed roots. The average length was 3.4 millimeters, and more than 90 percent lay in part in the inner bark. Some approached quite close to the surface of the wood (Figure 14), and many contained droplets of sap, but none attained the sapwood as reported by Becker (1). While some of the tunnels had been deserted by the beetles, 51.5 percent were still occupied. The direction of tunneling varied, with 45 percent up, 11.3 percent down, 5.5 percent transverse, and 34.3 percent oblique. In 3.8 percent the direction could not be determined, as apparently the beetles had not progressed far enough. The ratio of occupied to deserted tunnels for this particular group is rather high. On September 15, of 150 tunnels examined only 38 were occupied, or 25.3 percent. Many random samples gave even lower ratios.

FIGURE 14. Semi-schematic drawing of a longitudinal section through a bark tunnel, showing the relation to outer and inner bark layers, and to wood (about four times natural size). (From Kaston and Riggs.)

Though the bark tunnels are found most commonly on the trunk, they occur from the ground level all the way into the smaller limbs. Figure 15 shows a few in a one-inch branch, and we have seen them in a five-eighths-inch branch. To obtain some idea of their density at various levels on the trunk and leaders, a healthy tree was selected at random from among those standing in an area where beetles had emerged. The tree was quite straight, had a diameter breast high of 10 inches, and presented a fairly even surface to about 48 feet from the ground. Five levels were chosen at intervals of approximately 10 feet. At each level a section of bark 18 inches in height was carefully gone over, and only those tunnels noted which gave evidence of being recently made, *i.e.*, not from the previous years.

The results of the observations from September 6 to 9 inclusive are shown in Table 6. If these areas sampled are any indication, there must have been a very large number of beetles in the entire tree. The estimate given for the trunk includes only one of the main leaders. The density of these tunnels is greatest in the region between 12 and 33 feet above the

ground. The percentage of occupied tunnels is lowest in this same region. This would indicate that this part of the tree is preferred by the first beetles to emerge from breeding places. The upper and lower regions are attacked by the later emerging beetles, after some of the early ones have left to find suitable breeding places.

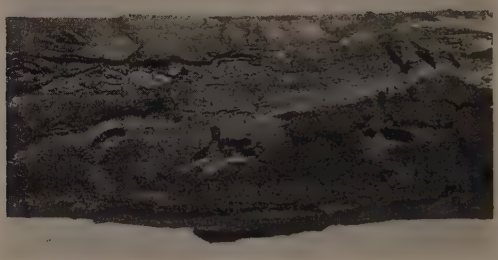

FIGURE 15. Small branch with bark tunnels, natural size. (From Kaston and Riggs.)

TABLE 6. BARK TUNNELS IN A HEALTHY ELM TREE AT VARIOUS LEVELS ABOVE THE GROUND

Height above Ground	Diameter in centimeters	Bark tunnels present			
		Total number	Density per square decimeter	Occupied	
				Number	Percent
2 ft. 6 in. to 4 ft.	26.8	49	1.3	15	30.6
12 ft. 6 in. to 14 ft.	20.4	423	14.4	50	11.8
22 ft. 6 in. to 24 ft.	14.1	266	13.8	29	10.9
31 ft. 10 in. to 33 ft. 4 in.	12	232	13.7	22	9.5
42 ft. 2 in. to 43 ft. 8 in.	6.2	58	6.6	10	17.2
Whole trunk..... (Estimated)	Bottom 30 Top 5	6753	8.3	818	12.1

Chapman (5) was the first to have noted that the adult beetles may overwinter, and that this hibernation takes place in healthy trees was pointed out by Becker (1). From our observations at regular intervals from July through the succeeding fall and winter, we are inclined to believe that there is no fundamental difference between hibernating tunnels and feeding tunnels. The beetles emerging early make their bark tunnels and then leave to construct egg galleries elsewhere. Those emerging later may construct bark tunnels late enough in the season to find their activity considerably retarded by the low temperatures prevailing during constantly

increasing portions of each day. Hence they do not leave to construct brood galleries, and their feeding tunnels now become their hibernating tunnels. The latter are, in general, longer than the former. It has also been observed that the ratio of unoccupied tunnels in the smaller branches, where the bark is thin, increases during October and early November. This is believed to indicate that some of the beetles had left to seek thicker bark in which to hibernate. Young adults which emerged as late as November 6 apparently made hibernating tunnels in thick bark without first feeding in thin.

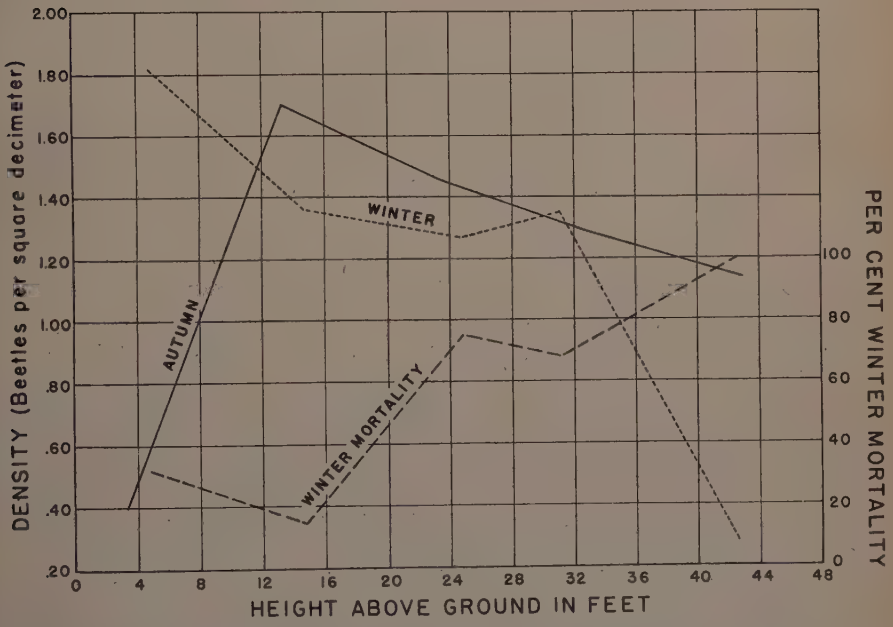

FIGURE 16. Curves showing the relation of the level at which beetles occur in bark tunnels to the density, and to winter mortality, etc.

Becker (1) reported late September as the time when first signs of hibernation were noticed, but he was then unaware that bark tunnels could be made earlier in the same places. To determine whether beetles were still active and feeding, the alimentary canal was dissected out and the ventriculus examined for food[1]. Although some beetles were found already inactive and with empty ventriculi on October 3, we found many still active and feeding right through to the end of October. It is evident that the prevailing local temperatures influence their activity on any given day, and that some of the beetles could have backed out of tunnels in September or earlier to construct new ones in which to hibernate.

[1] It may be mentioned parenthetically that experiments similar to those carried on with the larvae (p. 9) indicated a lack of ability to digest cellulose.

Hibernation

As discussed above, beetles may winter over as adults in bark tunnels made in live trees. Comparable areas of bark at various levels on the same tree used in the previous study were examined for hibernators about February 26, 1938. The beetles were carried into the laboratory and dissected to determine whether they were alive or dead. The results are shown in Table 7 and indicated graphically in Figure 16. The density and percentage of survival are greatest in the lower part of the tree where the bark is thick, and lowest in the upper part where it is thin. Taking the 137 beetles together, 56 were dead, a mortality of 41 percent. Of 116 adults collected at random from other localities, there were 71 dead, or 61 percent. Of 163 collected the previous season, 49 were dead, or 30 percent. The sum of these is 176, or 42 percent dead out of a total of 416 beetles.

TABLE 7. HIBERNATING BEETLES IN A HEALTHY TREE AT VARIOUS LEVELS ABOVE GROUND

Height above Ground	Diameter in centimeters	Beetles				
		Total*	Density per square decimeter	Live	Dead	Mortality percent
4 ft. to 5 ft. 6 in.....	24.8	64	1.82	40	19	32.2
14 ft. to 15 ft. 6 in.....	19.8	38	1.36	29	5	14.7
24 ft. to 25 ft. 6 in.....	12.7	23	1.27	5	15	75.0
30 ft. 4 in. to 31 ft. 10 in.	11.5	22	1.35	7	15	68.2
41 ft. 10 in. to 43 ft. 4 in.	5.1	2	.28	0	2	100.0

* This includes the few accidentally lost in the collecting process.

In addition to their hibernating in bark tunnels of live trees, in rare instances they may be found elsewhere. Ordinarily tenerals which are unable to emerge from pupal cells die sometime during the winter. However, a live teneral specimen was taken from a pupal cell at East River, March 26, 1936. Four were found in old egg galleries as follows: one at Mount Carmel, March 24, 1936; another at Groton, April 26, 1935; a third at Washington, April 1, 1936; and a fourth at Branford, March 13, 1938. The circumstances concerning the latter are particularly interesting. This tree had a diameter of 12 inches at breast height. It was among those examined on November 6, 1937, which at that time were partly dead. On the trunk were many beetles in bark tunnels, and also some in entrance holes leading to the wood surface. A few very short egg galleries could be found, but no eggs. On March 13, 1938, only one egg gallery had a beetle in it, but there were several beetles found in bark tunnels which were directly connected by the entrance tunnel to the gallery beneath. Several of the trees examined in the same area had similar connections of bark tunnels with egg galleries. The females found in these bark tunnels in

association with the egg galleries all had spermatozoa in the seminal receptacles in March. It seems likely, therefore, that the beetles started breeding tunnels late in the fall and then moved out into bark tunnels for the winter. We believe this to occur only very rarely, when a tree is in healthy enough condition in the fall to attract bark tunnel makers and then soon becomes receptive to them for breeding.

In the few cases in which eggs were found as late as November 28, we tested their viability by transferring 25 to the laboratory constant temperature and humidity room. All hatched out to normal larvae. All of the eggs found in similar galleries in these trees on March 13 must have been dead, for of the 42 placed in the constant temperature room, none hatched.

As is to be expected, the appearance of genitalia during hibernation differs from that during the breeding season. In the hibernating males the testes and seminal vesicles are more compact. Hibernating females have the ovarioles thin and the colleterial glands small.

Since, of course, the larvae hibernate in the bark of the dead limb in which the beetles have been breeding, they are much easier to find in quantity. All instars can be found but the older ones are more common. The larvae may continue to feed during the warmer parts of the day until quite late in November but slowly become more and more white as the food disappears from the intestinal tract.

Counts were made at intervals to determine the winter mortality. For the 1936–37 season, from a total of 2,190 larvae only 101 were dead, or 5 percent. In 1937–38, 38 were dead from a total of 1,656, or 2 percent.

Pupae are found only rarely during the winter. It would appear that ordinarily the lower temperatures of late fall prevent transformation to the pupal stage even when they do not prevent larval activity. Several logs which contained old larvae near pupation were placed in the insectary for observation. Of 22 pupae which were found in the late winter, 4 were dead; *i.e.*, a mortality of 18 percent. Of 55 pupae found outside, presumably lacking the partial protection of the insectary, there were 16 dead, or 29 percent.

Number of Generations

The number of generations and the time when the different stages are present throughout the year can be seen from the diagram, Figure 17. The dates of beginning activity naturally vary according to the temperature. Generally speaking, hibernating larvae begin to feed about the time the elm flowers appear. Some idea of the amount of variation may be gained from the following:

	1935	1936	1937	1938
Flowers began to appear....	April 3	March 26	April	March 23
Leaves began to appear....	April 25	April 20	May 1	April 15

The height of the peaks in Figure 17 does not represent the number of individuals for any given stage. The interval indicated between the first appearance of one stage and the earliest date for the succeeding stage is based upon our calculations of the duration of the stages according to the

average temperature at the particular time of year. Figures from the Weather Bureau office indicate the following average temperatures for New Haven:

May.....	57.9° F.	August.....	70.3° F.
June.....	66.6°	September..	63.7°
July.....	71.8°		

We proceeded on the assumption that the effect of temperature on developmental rates in the other stages was similar to that in the pupal stage. Although this assumption may be questioned, the results of the calculations checked well with field observations.

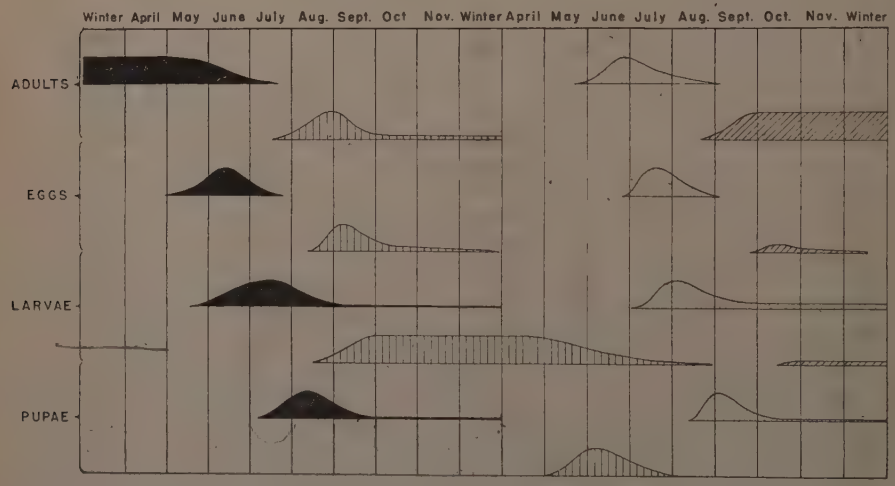

FIGURE 17. Diagram of the life cycle through two consecutive years. Solid black represents Generation A; vertical lines, Generation B; stippled areas, Generation C; and slanting lines, Generation D. The pupae of Generation A give rise to the adults of Generation B, and so on.

Starting with the A Generation adults, we find them hibernating during the first winter under consideration here. About the end of April the earliest ones start entering breeding material, and the latest will finish egg laying about the middle of July. The first eggs of this generation appear about the beginning of May, the first larva about the middle of May, and the first pupa during the second week of July. While most of these larvae will develop to pupae before late autumn, a few will be retarded and pass the winter in the larval stage. This represents a single generation per year. A still smaller number of pupae may overwinter. Ordinarily the first adults of the new (or B) Generation, from eggs laid by A, may be found as tenerals beginning about the middle of July. Most of the adults of this brood produce the eggs found in late August and September. Those emerging late may not enter to breed, but may be found in bark tunnels through the autumn and hibernate there during the winter. The eggs of

the B Generation give rise to the larvae which we believe to form the bulk of the hibernating population.[1] Eggs laid late in the fall (after the latter half of October), die during the winter.

The first tenerals of the C Generation, from hibernating larvae, appear toward the end of May and emerge from the bark about the middle of June. Their main oviposition period is in July and August. A few of the larvae from the eggs hatching late in the summer will winter over as such. The greatest number will give rise to the D Generation adults which winter over in bark tunnels, but a few of the adults will start brood tunnels. There is thus the possibility of having two generations during one year, for some of the eggs hatch before the onset of killing cold, as in the case of the B Generation. For the somewhat warmer climate of New Jersey, two generations per year appear to be more usual, according to Collins (6). Martin (25) believes one generation to be usual where he worked at Patterson, N.Y., but that locality hardly differs in topography and climate from the nearby Connecticut towns of New Fairfield and Danbury. We believe he has erred in his interpretation partly because he has restricted his observations to trap logs only.

NATURAL FACTORS OF CONTROL

Temperature

The factors involved in the control of this insect have not been thoroughly investigated. The climate of Connecticut is such that it plays very little part as a limiting factor. That severe winter temperatures may kill a large percentage of an overwintering bark beetle brood has been shown by Keen and Furniss (23). To gain some idea of the effects of low temperatures on *H. rufipes* several experiments were conducted, chiefly with the larvae, in which stage we believe by far the largest proportion of the population spends the winter. The method followed was a modification of the thermocouple technique given by Robinson (29, 30).

The thermojunction was placed in contact with the body of the specimen which lay at the bottom of a tube. The whole tube was immersed in a Dewar flask containing the cooling agent and the readings were made on a previously calibrated galvanometer scale. The temperature was lowered slowly and was allowed to drop beyond the freezing point to the supercooling point, as indicated by a deflection of the galvanometer due to the liberation of heat of crystalization. The temperature rises to the true freezing point, which can be read when the galvanometer makes a temporary halt before continuing down again. In Table 8 are given the results obtained with hibernating larvae. It is of interest to note that when these larvae were removed from the apparatus after being frozen, and allowed to attain room temperature, they all survived. Similar experiments with larvae that had already begun spring feeding showed a lessened resistance to the low temperatures. Furthermore, none survived the effects of the freezing. A third set of experiments run with pupae, which had just transformed from overwintering last instar larvae, surprisingly enough gave readings rather close to those of the latter. However, all the pupae died.

[1] Martin (25), in a paper which has just appeared, states that 80 to 90 percent of the population winters over in the adult stage. No evidence is given in support of this statement, which is contrary to our own observations. Nor is any evidence supplied to substantiate his statement that some larvae go through a "diapause" condition for more than 16 months so that they spend two winters in this stage. This would seem to require further explanation.

TABLE 8. RESULTS OF LOW TEMPERATURE EXPERIMENTS. AN ANALYSIS OF THE DIFFERENCES AMONG THE THREE GROUPS LISTED SHOWS THEM TO BE STATISTICALLY SIGNIFICANT

		Temperature degrees C.			
		Number of specimens	Highest	Lowest	Mean
Larvae: Overwintering	–supercooling....	35	–18.7°	–28.0°	–24.4° ± .2°
	–freezing.....	35	–10.0°	–23.5°	–16.4° ± .4°
Feeding.....	–supercooling....	36	– 6.3°	–20.3°	– 9.7° ± .5°
	–freezing.....	36	– 2.3°	–12.3°	– 4.7° ± .3°
Pupae:	–supercooling....	31	–14.5°	–23.3°	–21.7° ± .2°
	–freezing.....	31	– 7.8°	–18.6°	–13.0° ± .3°

Although winter air temperatures in Connecticut sometimes do get down to —24.4° C., equal to about —10° F., it must be remembered that the bark offers some protection. Not many overwintering larvae would be frozen. On the other hand it is possible for some larvae to die as a result of a cold spell coming on after they start feeding. The figures do not explain the scarcity of pupae during the winter, but they might in part account for the high mortality of this stage.

Moisture

The fact that this species rarely enters on the upper side of a horizontal limb in sunlight would indicate that it is intolerant of the higher temperatures on that side. Of course, there is the factor of dryness to be considered, and we have already pointed out (page 5) that a loss of more than half the original water content will render the logs unreceptive to attack. Once a brood is started, quick drying of a small limb, *i.e.*, about two inches in diameter, often kills the larvae before development can be completed.

Competition

There are instances where the density of egg galleries is so great that the larval tunnels coming off from them become confused while the larvae are still quite young. Many of these larvae are considerably retarded in their development, and no doubt many die. Besides overcrowding by individuals of their own species, many larvae lose out in competition with that most abundant of elm bark insects, *Saperda tridentata*, the larvae of which often ruin whole families of *H. rufipes*.

Predators

Hopkins (14) lists *Thanasimus dubius* Fabricius as a predator of *H. rufipes*, but the commonest predator in our experience is *Enoclerus*

nigripes Say (*quadriguttatus* auct.). Adults of *E. nigripes* can be found running about over the bark of elms most commonly in late May and June. They are voracious feeders, one specimen in the laboratory consuming five adults of *H. rufipes* in succession. They usually begin by disarticulating the head from the body, proceed from the head to the thorax, and end by cleaning out the abdomen, leaving only the cuticular structures. The entire process takes from 7 to 20 minutes.

Mating of *E. nigripes* probably occurs from the middle of May to the end of June, and a pair was observed *in copula* at Orange, June 17, 1935. Eggs can be found in June in the galleries of *H. rufipes*. On June 16, 1937, there were four *E. nigripes* eggs lying in the egg tunnel of an *H. rufipes* gallery. The latter had 20 larvae, none older than the second instar. The larvae of the predator feed on the bark beetle larvae to about the middle of August. They then migrate to the outer bark and construct a pupal cell. Emergence as adults occurs after the middle of September and the beetle hibernates in the adult stage. Specimens pupating in early September and placed in the constant temperature room at about 24° C. emerged in 12 or 13 days. The absence of parent bark beetles, especially the male, from egg galleries with eggs or young larvae can usually be attributed to their having been eaten by this predator.

While we have not actually observed the feeding of *Platysoma coarctatum* Leconte, it is reasonable to suppose from analogy with *P. punctigerum* Leconte, reported by Struble (32) to be a predator of various scolytids, that this species is also a predator. It is fairly common in bark containing old galleries of *H. rufipes*. Eggs were found in June in the larval tunnels. Pupation occurs in late August, not as in *E. nigripes* in a special pupal cell in the outer bark, but in the egg galleries of its prey.

Another, perhaps facultative, predator is the fly, *Lonchaea polita* Say, which is sometimes found in numbers. This also pupates in the egg galleries of *H. rufipes*.

Parasites

The commonest parasite encountered is the braconid, *Spathius canadensis* Ashmead (Figures 18 and 19). A list of the other hosts of this parasite has been published (Kaston and Becker, 20) and some notes on its habits have been recorded by the present author (18). This parasite has been observed to vary considerably in its abundance in different years. It seemed particularly abundant during 1935 and 1936, but has been noted only occasionally since then.

It has been found that beetle larvae of the penultimate and antepenultimate instars are attacked by *Spathius*, but by far the largest numbers are attacked in the last instar. Emerging adults vary considerably in size, and it is suggested that this may be due to the fact that development can evidently be completed on host larvae of different ages. The parasite attaches itself to the side or dorsum of the host (Figure 19 D), often with its head at the level of the host's metathorax.

This species hibernates as a prepupa in the cocoon, but, as this stage is also found in July, and young adults may emerge in early August, it would

appear that there are two broods per year. Exact data on the complete life cycle are lacking.

The parasitized host becomes entirely motionless and white in color, and, even though the parasite on it is quite small and inconspicuous, can easily be distinguished from unparasitized larvae. The cocoon of the

FIGURE 18. *Spathius canadensis*. Dorsal aspect of female, enlarged about 12 times. (From Kaston.)

parasite is pale yellow in color when first made, later turning to a dark brown. It is papery, covered with loose fibers, and usually has adhering to it particles of frass from the host's tunnel. The average dimensions of 17 cocoons were 4.5 by 1.4 millimeters. The pupal period is nine days at 24° C. The imago emerges from the bark through a circular hole about .75 millimeter in diameter, readily distinguished from the exit holes of its host which are about 1.25 millimeters in diameter.

The number of parasitized larvae seldom exceeds 25 percent in any one family, though in one instance we noted three-fourths of the larvae

with parasites. Usually the number of parasites is nearer 5 to 10 percent, and that only in certain localities, so that it may not play a rôle of great importance in the natural control of *H. rufipes*.

A parasite even less common and hence about which practically nothing is known was found to hibernate as a prepupa within the bodies of the overwintering adult beetles. This has been determined by A. B. Gahan as a new species and new genus of Pteromalidae. Each parasitized beetle has but a single parasite, which pupates without building a cocoon. The period of pupation is about 10 days at 24° C.

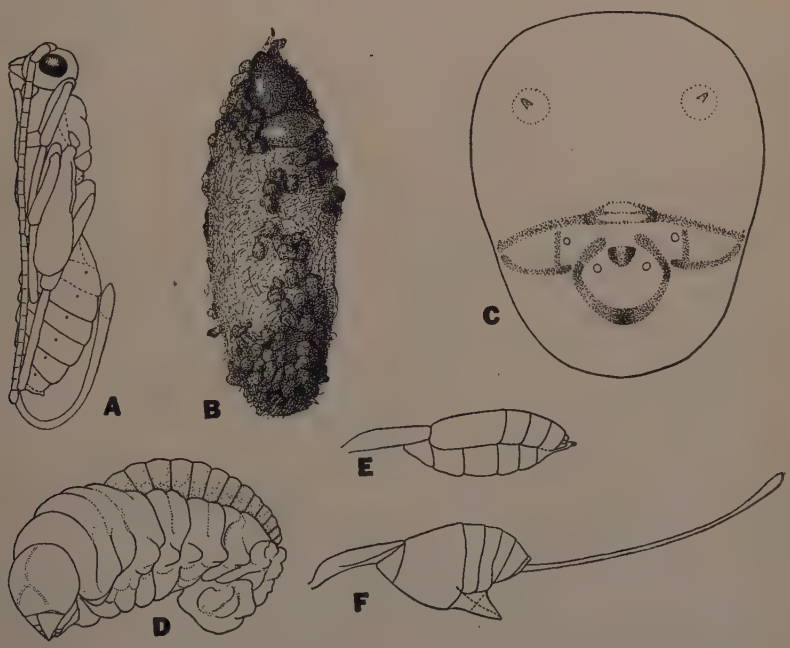

FIGURE 19. *Spathius canadensis*. A, pupa. B, cocoon. C, anterodorsal aspect of the prepupal head. D, feeding larva on its host. E, lateral aspect of the abdomen of an adult male, and F, of an adult female. (From Kaston.)

Nematodes have been reported from various Scolytidae. While Steiner (31) supposes that they may destroy beetles, he gives no data. Oldham (27) points out that the presence of nemas in the body cavity can have the effect of reducing the size of the gonads and even lead to sterility.

Approximately four-fifths of the adult beetles examined from mixed localities had nemas in the coelomic cavity. They were as often found in one sex as the other. In only a very few was there any diminution in the size of the gonads, which might be attributed to the nemas. Of the many larvae and pupae examined none were found to contain nemas. One batch of prepupae was removed to dishes and obliged to pupate and emerge as adults free of all bark. After the tenerals had hardened somewhat they were dissected and examined. Of 44 examined 36 had nemas. It is obvious,

therefore, that the nemas must be present in the larvae and pupae, but in some minute embryonic or larval form not readily seen, and only develop when the beetles reach the adult stage.

Mites are often found in the galleries of *H. rufipes* and a number of species are carried about on the bodies of the beetles. The significance of these as possible carriers of the Dutch elm disease has been discussed by Jacot (15, 16). In some galleries nearly every beetle had one or more young specimens of *Uropoda* sp. attached to it. These are probably not parasitic, but are merely being transported about. They may be attached to the abdominal sternites or the elytra.

Attached to the intersegmental membrane behind the prosternum are often found several specimens of *Pediculoides dryas* Vitzthum. These are apparently actual parasites but do not seem to be as injurious to their host as the congener *P. ventricosus* is to its hosts. Sometimes the mites are seen eating the eggs, and occasionally the larvae of the beetle. In the case of the latter, since mites have been found only on dead larvae, it is not clear whether they actually killed the larvae or are merely saprozoic.

ASSOCIATED FAUNA

Besides those already referred to as predators or parasites of the native elm bark beetle, there are numerous other insects associated with it under the bark, and a list has been published (Kaston, 19).

Perhaps the most important associate is the smaller European elm bark beetle, *Scolytus multistriatus* Marsham. In this species the breeding habits are quite similar to those of *H. rufipes*. They differ in that the egg galleries of the former are parallel to the grain of the wood, the larval galleries in general lie across the grain, and the galleries score the wood surface much more than do those of the native beetle. The European species tolerates a greater degree of dryness and heat, as evidenced by its being found more commonly than the latter on the upper sides of branches in which the native beetle occurs, as well as in branches of smaller diameter.

The elm snout beetles, *Magdalis barbita* Say and *M. armicollis* Say, are fairly common, especially in the smaller, drier limbs.

Probably the most common and abundant insect found in elm bark is the cerambycid, *Saperda tridentata*. The larvae may be found in the very moist bark of a limb or tree which has just recently died, as well as at the other extreme where the bark is too dry for any scolytids. It competes successfully with *H. rufipes* in consuming bark for food and is thus a factor in keeping down the numbers of the latter species.

In old bark from which most of the *H. rufipes* have emerged, the larva of the melandryid, *Synchroa punctata* Newman, is quite common. It presumably feeds on the decaying bark.

SUMMARY

The native elm bark beetle, *Hylurgopinus rufipes* (Eichhoff), is known to occur over most of the eastern and middle western United States. In Connecticut there are most commonly one and a half generations per year.

Overwintering larvae give rise to beetles whose progeny hibernate during the following winter as adults. Likewise, overwintering adults give rise to beetles whose progeny hibernate the next winter as larvae. There may also be two generations per year. In a few cases only one generation occurs, especially when larvae in crowded bark are unduly retarded in their development. Eggs do not survive the winter, and only a very few individuals hibernate in the pupal stage.

For breeding purposes the beetles prefer shaded limbs over two inches in diameter which have not lost more than half their original water content. The majority of the egg galleries are "V" shaped, biramous, and tend to run across the grain. The average length appears to be 30 millimeters, and the average number of eggs per female about 60. Mortality from various causes reduces the brood so that only about 15 young beetles emerge per family. Parent beetles raise only a single brood and die in the egg gallery.

Ordinarily, eggs hatch in from 6 to 12 days. The larval stage varies in length from a minimum of 29 days, at 24.5° C., to about 40 or 50 days, in the field during the summer months. It has been shown that the number of instars may vary but it is believed that the usual number is five or, less commonly, six. It is not possible to determine the number by the application of Dyar's Law to mixed lots of larvae taken at random from various localities in the field. The larval galleries tend to run with the grain and the rate of tunneling was found to be quite variable with different larvae.

The pupal period of 8 to 12 days follows a quiescent prepupal period of two or three days. Emerging young beetles fly to healthy elms to feed in bark tunnels before seeking material in which to breed. There is evidence to indicate a flight range of at least a mile, though presumably the beetles will attack the nearest available material. The bark tunnels are here considered analogous to the well-known crotch and twig feeding injuries of *Scolytus multistriatus* Marsham, and hence important in relation to the spread of the Dutch elm disease. They are in the bark alone, and do not touch the surface of the wood. Those made for hibernation tend to be longer and are more often in thicker bark than the otherwise similar feeding tunnels.

Low temperatures in winter have little effect on the hibernating larvae, but only about half of the hibernating adults survive. Dryness and competition, both with other *H. rufipes* larvae and the larvae of *Saperda tridentata*, probably account for the high mortality during the growing season. Predators and parasites appear to be of little significance.

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